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RESEARCH ARTICLE

Non-native freshwater fishes in Guatemala, northern Central America: introduction sources, distribution, history, and conservation consequences

Diego J. Elías[1,2], César E. Fuentes-Montejo[3,4], Yasmín Quintana[5,6], Christian A. Barrientos[6,7]

1 *LSU Museum of Natural Science (Ichthyology), Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803 USA*
2 *Colección ictiológica, Sistema de Colecciones Biológicas, Escuela de Biología, Universidad de San Carlos de Guatemala, Zona 12 Ciudad Universitaria, Guatemala, Guatemala*
3 *Escuela de Biología, Facultad de Ciencias Químicas y Farmacia, Universidad de San Carlos de Guatemala; Edificio T10, Ciudad Universitaria, zona 12, Guatemala, 01012, Guatemala*
4 *Department of Biological Sciences, DePaul University, Chicago, IL 60614, USA*
5 *Department of Ecology and Conservation Biology, Texas A&M University, College Station, Texas, 77843 USA*
6 *Centro de Estudios Conservacionistas, Facultad de Ciencias Químicas y Farmacia, Universidad de San Carlos de Guatemala, Guatemala, 01010, Guatemala*
7 *Mesoamerican Marine Program, WCS, 1755 Coney Drive, 2nd Floor Coral Groves, Belize, Belize*

Corresponding author: Diego J. Elías (delias@lsu.edu)

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Abstract

Non-native freshwater fishes have been introduced to Guatemalan freshwater ecosystems since the beginning of the last century without prior risk assessment or subsequent evaluation of their impacts. We synthesized historical records, and distributional data from a literature review, online databases and museum records of non-native freshwater fishes in Guatemala. We found records for 22 non-native freshwater fishes with the oldest records dating back to 1926. Non-native freshwater fishes were recorded in 64% of the river sub-basins in Guatemala and we identified that at least 12 species have established populations. The Jaguar guapote (*Parachromis managuensis*) and Tilapias (*Oreochromis* spp.) are the most widespread non-native fishes. The species of non-native freshwater fishes introduced indicates that they are human selected (e.g., for farming purposes). Our work shows that aquaculture has been the major driver of introductions in the country, but aquarium release has become an important

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source in the last 20 years. Given the potential impact of non-native freshwater fishes on native fauna and ecosystems, we highlight an urgent need to assess their ecological effects, as well as to establish a fish fauna monitoring program in Guatemala to detect new introductions. Government and non-governmental agencies should promote the use of native species to supply fish demands in alignment with environmental policies and the objectives of the fishing agency in Guatemala.

Keywords
Exotic species, inland waters, invasive fishes, management, northern Neotropics

Introduction

Non-native freshwater fishes -NNFF- have been intentionally introduced around the world for the enhancement of sport and commercial fisheries (Rahel 2007), as well as for biocontrol (Pípalová 2006; Walsh et al. 2016). Other common causes of NNFF introductions includes accidental escapes from aquaculture facilities or intentional release by aquarists (Welcomme 1992; Duggan et al. 2006; Rahel 2007). Introduced species have the potential to become invasive (*sensu* Blackburn et al. 2011), threaten biodiversity and disrupt ecosystem functioning (e.g., predation, competition, habitat degradation; Sala et al. 2000; Cambray 2003; Strayer 2010; Simberloff 2015). Despite these negative effects, introducing NNFF for aquaculture and stocking purposes is a common practice, particularly in developing regions such as Central America. These introductions are often made without prior risk assessment and subsequent management. Neither the benefits nor the negative impacts of these practices have been assessed in the northern Neotropics (but see McCrary et al. 2007; Capps and Flecker 2013a, 2015; Capps et al. 2015). Additionally, information regarding the distribution or the establishment status of NNFF in the region is either scarce or unpublished.

Guatemala, located in northern Central America (Fig. 1), possesses three major drainages: Pacific coast, Atlantic coast, and Gulf of Mexico; that encompass 33 river sub-basins (MAGA 2009; Suarez 2011; Fig. 1). Approximately 60% of these river sub-basins are shared with neighboring countries (Mexico, Belize, Honduras and El Salvador; Fig. 1). The continental ichthyofauna of Guatemala comprises 246 species of which 18 are endemic to the country (Kihn-Pineda and Cano 2012). Fish assemblages in the Gulf of Mexico drainage possess high levels of endemism in Central America (Matamoros et al. 2015; Elías et al. 2020). Despite the ichthyofauna in the country having been widely studied (see Kihn-Pineda et al. 2006 and references therein) and research having intensified in the past 20 years (Willink et al. 2000; Granados-Dieseldorff et al. 2012; Barrientos et al. 2015; Quintana et al. 2016; Barrientos et al. 2018; Barrientos et al. 2019; Quintana et al. 2019; Quintana et al. 2021), several aquatic systems are still underexplored. Recently, unique molecular diversity has been uncovered (e.g., Elías et al. 2020; Elías et al. 2022), and species are still being discovered (e.g., Dallevo-Gomes et al. 2020). Currently, 15 NNFF have been reported across the country (Kihn-Pineda and Cano 2012; Elías et al. 2018; Gaitán et al. 2020) but their distribution and status have not been assessed.

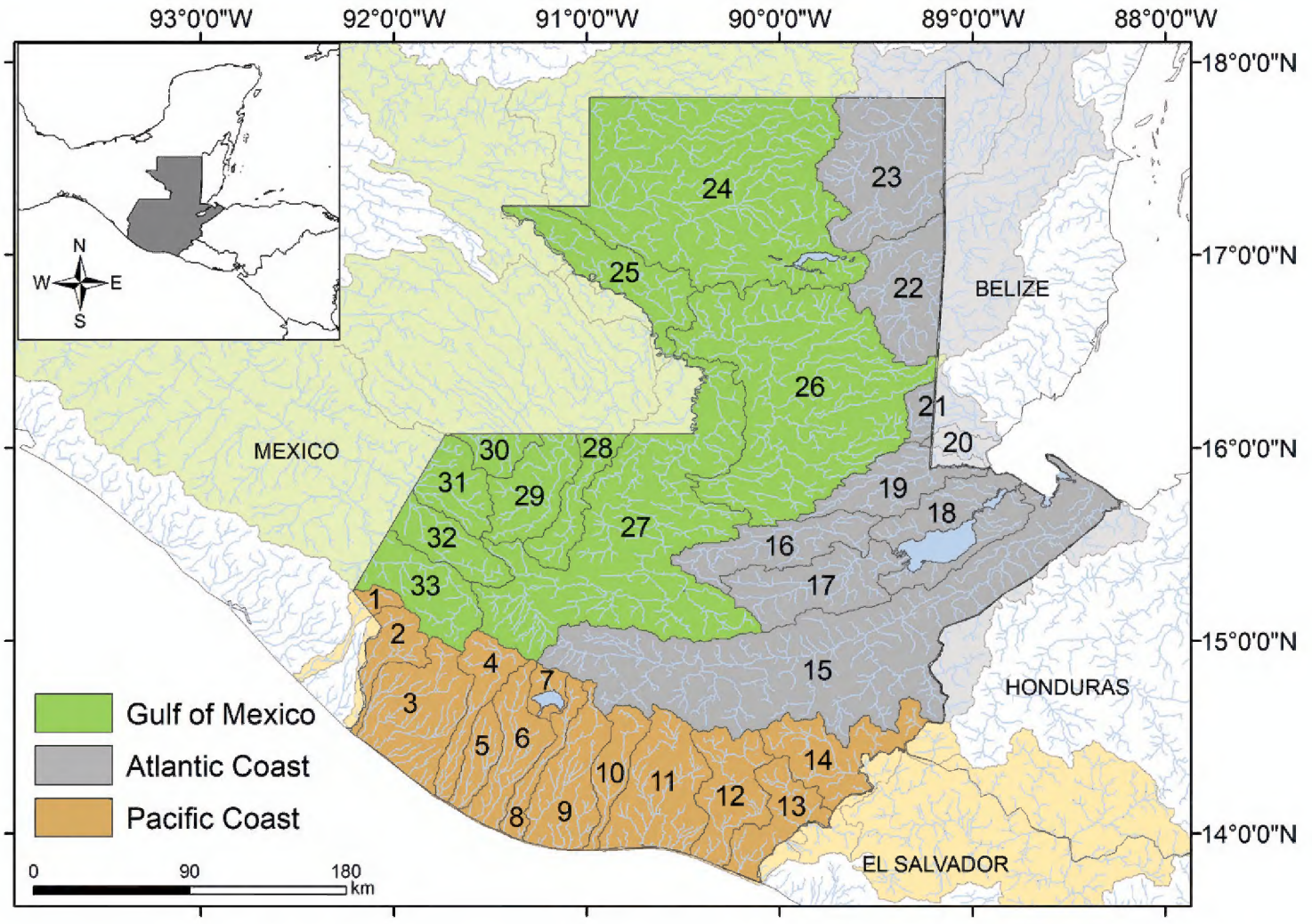

Figure 1. Guatemalan major drainages and river sub-basins, following Suarez (2011). The three major drainages are color shaded. Pacific coast (light brown), Atlantic coast (grey), and Gulf of Mexico (green). The map shows the 33 river sub-basin boundaries, within the political boundaries of Guatemala. River sub-basins shared with neighboring countries are shown in a lighter shade of color. River sub-basins: Río Coatán (1)*, Río Suchiate (2)*, Río Ocosito-Naranjo (3), Río Samalá (4), Río Sis-Icán (5), Río Nahualate (6), Lago de Atitlán (7), Río Madre Vieja (8), Río Coyolate (9), Río Achiguate (10), Río María Linda (11), Río Los Esclavos (12), Río Paz (13)*, Río Lempa (14)*, Río Motagua (15)*, Río Cahabón (16), Río Polochic (17), Lago Izabal-Río Dulce (18), Río Sarstún (19)*, Río Temash (20)*, Río Moho (21)*, Río Mopán-Belice (22)*, Río Hondo (23)*, Río San Pedro-Candelaria (24)*, Río Usumacinta-main channel (25)*, Río La Pasión (26)*, Río Salinas-Chixoy (27)*, Río Xaclbal (28)*, Río Ixcán (29)*, Río Pojom (30)*, Río Nentón (31)*, Río Selegua (32)*, Río Cuilco (33)*. Asterisk denotes sub-basins that are shared with neighboring countries. Major lakes in Guatemala: Lake Atitlán (sub-basin 7), Lake Izabal (sub-basin 18), Lake Petén Itzá (sub-basin 24), Lake Lachuá (sub-basin 27).

Agricultural agencies have promoted the pond fish culture and the stocking of NNFF in freshwaters ecosystems to support continental fisheries and local food supply in Guatemala since the 1950s (Hughes 1974). Initially, most governmental efforts focused on species like the Jaguar guapote (*Parachromis managuensis*: Cichlidae), Carp (*Cyprinus carpio*: Cyprinidae), and the Mozambique tilapia (*Oreochromis mossambicus*: Cichlidae) (Hughes 1974). Some centrarchids (e.g., Largemouth bass, *Micropterus salmoides*) were also introduced by the government with advice from the United States Fish and Wildlife Service (Holloway 1950; Miles 1967). These initiatives took place prior to the establishment of the Guatemalan Fishing Agency-DIPESCA (i.e., Dirección de Normatividad de la Pesca y Acuicultura) in 1975. This agency has continued using NNFF for aquaculture and the stocking of

freshwater systems across the country. In addition, popular species in the aquarium trade have been reported (Kihn-Pineda et al. 2006; Kihn-Pineda and Cano 2012; Ariano-Sánchez et al. 2017; Elías et al. 2018; Gaitán et al. 2020). Some of these species are considered potentially invasive (e.g. *Pterygoplichthys* spp.) and are regulated to prevent new introductions across the country (CONAP 2011) although these protocols are based on precautionary principles and are seldom enforced.

The introduction and establishment of NNFF poses a further threat to the fish diversity in Guatemala that is already vulnerable due to habitat destruction, water pollution, and overfishing. The lack of a synthesis that encompasses the origin, distribution and potential impacts of NNFF across river sub-basins in the country hinders the development of guidelines for their management (Zaret and Paine 1973; McKaye et al. 1995; Bedarf et al. 2001; Esselman et al. 2013). Thus, the main goal of this study was to synthesize information available on NNFF in Guatemala, and to fill knowledge gaps on the topic. We hypothesized that aquaculture is the main cause of introductions of NNFF in Guatemala. Specifically, in this study we 1) compiled and analyzed information on the introductions of NNFF in Guatemala based on museum records, peer-reviewed publications, and grey literature, 2) updated the checklist of NNFF in Guatemala, 3) generated maps of their known records, and 4) provided a timeline, source of introduction and current status of NNFF in the country. Finally, we provide an overview of the consequences of NNFF introductions for the country and perspectives for their management.

Methods

Data acquisition and curation

To compile information on the number NNFF and their known records we conducted an exhaustive literature review including both published peer-reviewed literature and grey literature (i.e., reports from governmental and non-governmental agencies; undergraduate theses from Guatemalan universities; and meeting abstracts). We started our searches by reviewing publications of continental fishes in Guatemala from the early 1900s to the present. We complemented our literature review with a query of online databases (i.e., Fishbase 2020; FAO 2021) that contain records of introductions of NNFF in Guatemala.

We also compiled records of NNFF in Guatemala from local scientific collections, with acronyms following Sabaj (2020): Sistema de Colecciones Biológicas, Escuela de Biología, Universidad de San Carlos de Guatemala (**USAC**) and Universidad del Valle (**UVG**). We also performed online queries on public databases from international museum collections (i.e., AMNH 2020; Fishnet2.net 2020; GBIF.org 2020; IDigBio 2020). We filtered our searches to include only records that have discoverable voucher specimens. We generated a combined database of records from all our local and online queries, which was filtered to only include records of NNFF (Suppl. material 1: Table S1). We curated our combined database to include museum records (i.e., catalog number) only once to avoid duplications

of records due to the search of different data aggregators for our online queries. We contrasted our curated database (see Suppl. material 1: Table S1) with records of NNFF cited in the literature, to include and analyze each record only once. We included field observations of NNFF by the authors. These were recorded during recent surveys conducted across 14 river basins (200 localities) in Guatemala from 2016 to 2019. The author's field observations include voucher specimens that are in the process of being catalogued in museum collections (i.e., LSUMZ, SLU, TCWC; Suppl. material 1: Table S1) and observational records (e.g., collected individuals by the authors that were not preserved). The final database included information on the date of the record, geographic information (if available), river sub-basin and drainages of each record. We classified the records as vouchered (i.e., museum records) and non-vouchered (i.e., literature or observational records). The curated database analyzed is available as Suppl. material 1 (i.e., Suppl. material 1: Table S1).

Timeline, cause, and status of introductions

We classified the records of NNFF in three time periods: 1) Pre-1950 introductions prior to the development of governmental policies for the introduction of NNFF in Guatemala, 2) 1950–1999 introductions stimulated by the government and the creation of the Guatemalan Fishing Agency, and 3) 2000 to 2019 "contemporary" introductions. This historical analysis allowed us to identify temporal trends and to reconstruct the timeline of introductions of NNFF in Guatemala.

To describe the cause of the introduction for each species we categorized and quantified the relative contribution of two sources (i.e., aquaculture and aquarium source). We acknowledge that introduction for recreational fishing purposes was suggested by Meek (1908) but to our knowledge, introductions for this sole purpose were not implemented in Guatemala. We defined "aquaculture source" as NNFF that were introduced for fisheries purposes or to support local food supply, whether these fishes are raised in "farms" or "cages" at an industrial and small scale in aquatic ecosystems. We considered aquaculture introductions as either species released by the government for stocking purposes or ones that accidentally escaped from aquaculture facilities (e.g., due to flooding during extreme weather). We defined "aquarium source" as NNFF that are common in the aquarium trade that we inferred were intentionally released or that escaped into aquatic environments. We defined species of NNFF as "established" if a) we found evidence of younglings, juveniles, or adults individuals in reproductive stages present in aquatic ecosystems or b) if the species are known to be part of the target species of the local continental fisheries in the country.

Distribution of non-native freshwater fishes

We utilized the 33 river sub-basins sensu Suarez (2011) as analytical units. River sub-basin boundaries and the river network follow Lehner and Grill (2013). We categorized each river sub-basin to belong to one of the three main drainages in

the country, Pacific coast (14 sub-basins), Atlantic coast (9 sub-basins), and Gulf of Mexico (10 sub-basins) drainages (Fig. 1). We plotted geo-referenced records to identify the major drainages and river sub-basins where NNFF have been recorded. The use of river sub-basins allowed us to further include records that do not possess geographic coordinates but do possess locality information (e.g., river sub-basin) of the record that we can confidently assign to a unique river sub-basin in Guatemala. With this information we quantified the number of NNFF present in each river sub-basin across the country. Records without geographic coordinates or detailed locality information were excluded from the distributional analysis but were kept for the species list and the analysis of the timeline of introductions.

Taxonomic uncertainties

All recorded NNFF were listed with their current valid taxonomy following Fricke et al. (2021) and we provide their common names in English and Spanish. Some records were included only at the generic level (e.g., records without species level identification). When vouchers specimens were available and the taxonomic identification was doubtful, we tried to confirm their identification (mainly from records from Guatemalan collections). Currently, some genera still have unresolved taxonomic issues (e.g., *Hypostomus* and *Pterygoplichthys*, J. Armbruster pers. comm.), from which we took a conservative approach and we included these records identified only at the generic level. We took the same conservative approach for non-vouchered records for which species level identity is uncertain or not available. To account for this uncertainty when multiple records in a river sub-basin were identified only at the generic level, we counted them as one species. If multiple records of the same genus are reported at the generic and species level in the same river sub-basin we treated the records identified only at the genus level with the same taxonomic identity as the records at the species level. This conservative approach allowed us to include records with taxonomic uncertainty and to avoid overestimating the number of NNFF reported in each river sub-basin.

Results

Non-native freshwater fishes in Guatemala

We compiled a total of 283 records of NNFF; 171 represent museum records and 112 represent records compiled from the literature review and by the author's field observations (see Suppl. material 1: Table S1). Ninety percent (n = 255) of the records are geo-referenced and 94% (n = 266) included the date of the record. We identified 22 NNFF belonging to nine different families that have been introduced in Guatemala (Table 1), of which 19 of these species have detailed geographic information within the country (see Suppl. material 1: Table S1). The families with the highest number of NNFF recorded are Cichlidae with six species and Centrarchidae with four species. They are followed by the family Loricariidae with three species

Table 1. Non-native freshwater fishes reported in Guatemala and causes of their introduction. Drainages and number of river sub-basins where reports occur and the earliest year recorded are enlisted. Status = establishment status. Ac = Aquaculture release, Re = Aquarium release, N/A = Not Available. Drainages: A = Gulf of Mexico, B = Atlantic coast, C = Pacific coast. E = established, NE = not established, U = Unknown.

Taxa	Common name (Spanish common name)	Main source of introduction	Year reported	Drainage	No. of basins	Reference	Voucher deposited	Status
Cyprinidae								
Carassius auratus (Linnaeus, 1758)	Goldfish (Carpa dorada o Pez dorado)	Re	1946	A, B	2	Valdez-Moreno et al. 2005; Kihn-Pineda et al. 2006; Kihn-Pineda and Cano 2012	USNM, MCZ	U
Cyprinus carpio Linnaeus, 1758	Common carp (Carpa común)	Ac	1926	A, B, C	4	Miles 1967; Welcomme 1988; Kihn-Pineda et al. 2006; Barrientos and Quintana 2012; Kihn-Pineda and Cano 2012; FAO 2021	USNM, LSUMZ	E
Xenocyprididae								
Ctenopharyngodon idella (Valenciennes, 1844)	Grass carp (Carpa china o Carpa herbívora)	Ac	1979	A, C	4	Willink et al. 2000; Valdez-Moreno et al. 2005; Kihn-Pineda et al. 2006; Kihn-Pineda and Cano 2012; FAO 2021	AUM, FMNH, SLU	E
Serrasalmidae								
Colossoma macropomum (Cuvier, 1816)	Tambaqui (Cachama)	Ac	1989	N/A	N/A	FAO 2021	N/A	U
Piaractus brachypomus (Cuvier, 1818)	Pirapitinga (Pacu)	Re	2017	A	1	Elías et al. 2018	FMNH	U
Ictaluridae								
Ictalurus punctatus (Rafinesque, 1818)	Channel catfish (Pez gato americano o Bagre del canal)	Ac	1940's	A, B	2	Holloway 1950; Kihn-Pineda et al. 2006; Kihn-Pineda and Cano 2012	N/A	U
Loricariidae								
Pterygoplichthys disjunctivus (Weber, 1991)	Vermiculated sailfin catfish (Plecóstomo)	Re	2011	A, C	2	Barrientos and Quintana 2012; Penados Saravia 2014; Ariano-Sánchez et al. 2017; Villavicencio 2017	USAC, CEMA	E
Pterygoplichthys pardalis (Castelnau, 1855)	Amazon sailfin catfish (Pez diablo o Pleco)	Re	2011	A	2	Kihn-Pineda and Cano 2012; Penados Saravia 2014; Ariano-Sánchez et al. 2017	USAC, CEMA	E
Pterygoplichthys sp.	Sailfin catfish (Pez diablo o Pleco)	Re	2009	A, B, C	6	UNIPESCA 2010; Barrientos and Quintana 2012; Penados Saravia 2014; Ariano-Sánchez et al. 2017; Gaitán et al 2020	USAC, CEMA, ECO-CH, ECO-S-CP, LSUMZ	---
Hypostomus sp	Plecostomus (Pez diablo o Plecostomo)	Re	1996	B	1	N/A	UVG	NE
Salmonidae								
Salmo trutta Linnaeus, 1758	Sea trout (Trucha marina)	Ac	1993	N/A	N/A	FAO 2021	N/A	NE
Oncorhynchus mykiss (Walbaum, 1792)	Rainbow trout (Trucha arcoíris)	Ac	1982	A	1	Kihn-Pineda et al. 2006; Crawford and Muir 2008; Kihn-Pineda and Cano 2012; López Paredes 2013; FAO 2021	N/A	U
Poeciliidae								
Poecilia reticulata Peters, 1859	Guppy	Re	2006	B, C	2	Kihn-Pineda et al. 2006; Kihn-Pineda and Cano 2012	N/A	U
Centrarchidae								
Lepomis gibbosus (Linnaeus, 1758)	Pumpkinseed	Ac	1960	C	1	Welcomme 1988; FAO 2021	N/A	NE
Lepomis macrochirus Rafinesque, 1819	Bluegill (Perca)	Ac	1954	C	3	Miles 1967; Kihn-Pineda et al. 2006; Barrientos and Quintana 2012; Kihn-Pineda and Cano 2012	UVG, USAC, ZMH, LSUMZ	E

Taxa	Common name (Spanish common name)	Main source of introduction	Year reported	Drainage	No. of basins	Reference	Voucher deposited	Status
Micropterus salmoides (Lacépède, 1802)	Largemouth bass (Lobina negra)	Ac	1954	B, C	4	Miles 1967; Welcomme 1988; Kihn-Pineda et al. 2006; Barrientos and Quintana 2012; Kihn-Pineda and Cano 2012	USAC, UVG, ZMH, LSUMZ, FMNH	E
Pomoxis nigromaculatus (Lesueur, 1829)	Black crappie (Mojarra negra)	Ac	1958	B, C	2	LaBastille 1974; Kihn-Pineda et al. 2006; Barrientos and Quintana 2012; Kihn-Pineda and Cano 2012	UVG	E
Cichlidae								
Parachromis dovii (Günther, 1864)	Wolf cichlid (Guapote)	Ac	1974	C	1	N/A	UMMZ	E
Parachromis managuensis (Günther, 1867)	Jaguar guapote (Guapote o Guapote tigre)	Ac	1934	A, B, C	11	Holloway 1950; Welcomme 1988; Kihn-Pineda et al. 2006; Kihn-Pineda and Cano 2012; FAO 2021	USAC, UMMZ, UA, FMNH, AUM, UVG, NRM, UF, LSUMZ, ECO-S-CP, SLU	E
Oreochromis aureus (Steindachner, 1864)	Blue tilapia (Tilapia azul)	Ac	1974	A, B, C	7	Welcomme 1988; Valdez-Moreno et al. 2005; Kihn-Pineda et al. 2006; Kihn-Pineda and Cano 2012	USAC, ECO-CH	E
Oreochromis mossambicus (Peters, 1852)	Mozambique tilapia (Tilapia del Mozambique)	Ac	1955	A, B, C	7	Welcomme 1988; Kihn-Pineda et al. 2006; Kihn-Pineda and Cano 2012	UMMZ, FMNH, AMNH, USAC, SLU	E
Oreochromis niloticus (Linnaeus, 1758)	Nile tilapia (Tilapia del Nilo o Tilapia gris)	Ac	1954	A, B, C	3	Welcomme 1988; Barrientos and Quintana 2012; Palomo Cortez et al. 2016; FAO 2021	USAC	E
Oreochromis urolepis (Norman, 1922)	Wami tilapia	Ac	1974	N/A	N/A	Welcomme 1988; FAO 2021	N/A	NE
Oreochromis sp.	Tilapia	Ac	1989	A, B, C	7	López Paredes 2013; Palomo Cortez et al. 2016; FAO 2018	UF, USAC, LSUMZ, SLU, FMNH	---

(Table 1). The families Cyprinidae, Salmonidae, and Serrasalmidae are present with two species each, and finally the families Ictaluridae, Poeciliidae, and Xenocyprididae with one species each (Table 1). Out of the 22 NNFF reported, 55% (12 species) were identified to have established populations in Guatemala (Table 1).

Timeline, cause, and status of introductions of freshwater fishes in Guatemala

Five percent (12) of the records were reported during the pre-1950 period; 24% (64) were reported within the 1950–1999 period; and 71% (190) correspond to the contemporary period (Fig. 2). The first species of NNFF recorded in Guatemala was the Common carp (*Cyprinus carpio*) in 1926 (Fig. 3; Table 1) but there is no information regarding the locality of this record. The second species of NNFF recorded was the Jaguar guapote (*Parachromis managuensis*) which was introduced in 1934 in the river sub-basin Río Los Esclavos (Fig. 3; Table 1) in the Pacific coast. In the 1940s the Goldfish (*Carassius auratus*) and the Channel catfish (*Ictalurus punctatus*) were recorded in Río Cahabón, Río Motagua, Lago de Izabal-Río Dulce river sub-basins (Atlantic coast), and the Río Salinas-Chixoy in the Gulf of Mexico (Fig. 3; Table 1). In the 1950s

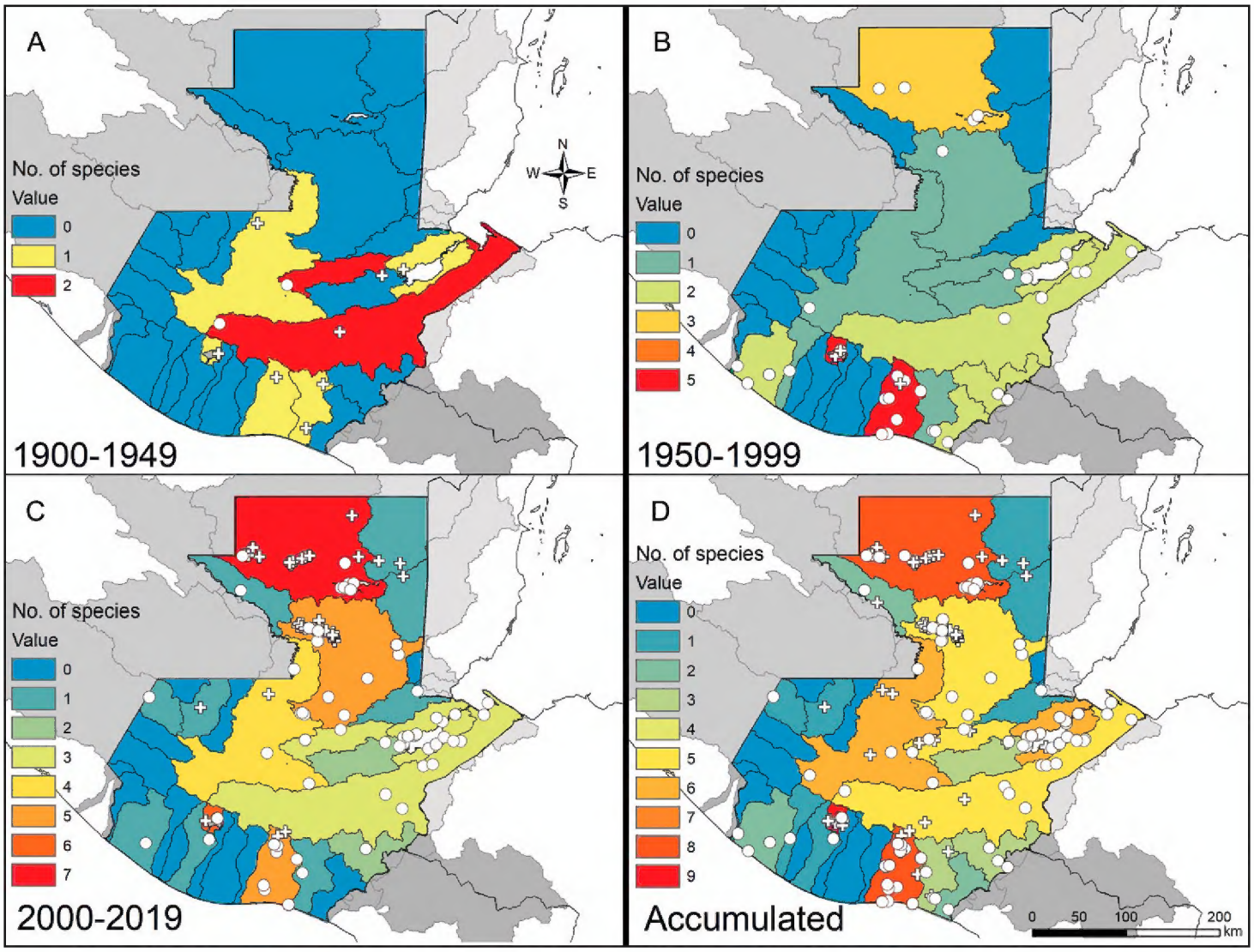

Figure 2. Chronological heat maps of records of non-native freshwater fishes in the 33 river sub-basins in Guatemala. Records are shown in three time periods (see methods) **A)** previous to 1950, **B)** 1950 to 1999, **C)** 2000 to 2019. The accumulated records and number of non-native fishes per river sub-basin are presented in panel D. Circles represent records with voucher specimens and cross marks represent records without a voucher specimen.

three species of centrarchids (i.e., *Lepomis macrochirus*, *Micropterus salmoides*, and *Pomoxis nigromaculatus*) were introduced in Lago de Atitlán and Río María Linda river sub-basins in the Pacific coast. Two species of tilapia (i.e., *Oreochromis niloticus* and *O. mossambicus*) were also introduced in the 1950s, but we did not find information regarding the locality of these introductions (Fig. 3; Table 1). In 1960, another centrarchid species, the Pumpkinseed (*Lepomis gibbosus*) was introduced in Lago de Atitlán sub-basin in the Pacific coast (Fig. 3; Table 1). In the 1970s four more species were introduced, including the Grass carp (*Ctenopharyngodon idella*), the Wolf cichlid (*Parachromis dovii*), and two more species of tilapia (*O. aureus* and *O. urolepis*) from which we did not find information regarding the localities of introduction (Fig. 3; Table 1). In the 1980s, the Tambaqui (*Colossoma macropomum*) and the Rainbow trout (*Oncorhynchus mykiss*) were introduced (Fig. 3; Table 1). In the 1990s the Plecostomus (*Hypostomus* sp.) and the Sea trout (*Salmo trutta*) were introduced. Finally, from the year 2000 to the present, four NNFF were recorded in aquatic systems in Guatemala including the Guppy (*Poecilia reticulata*), two species of sailfin catfish, Vermiculated

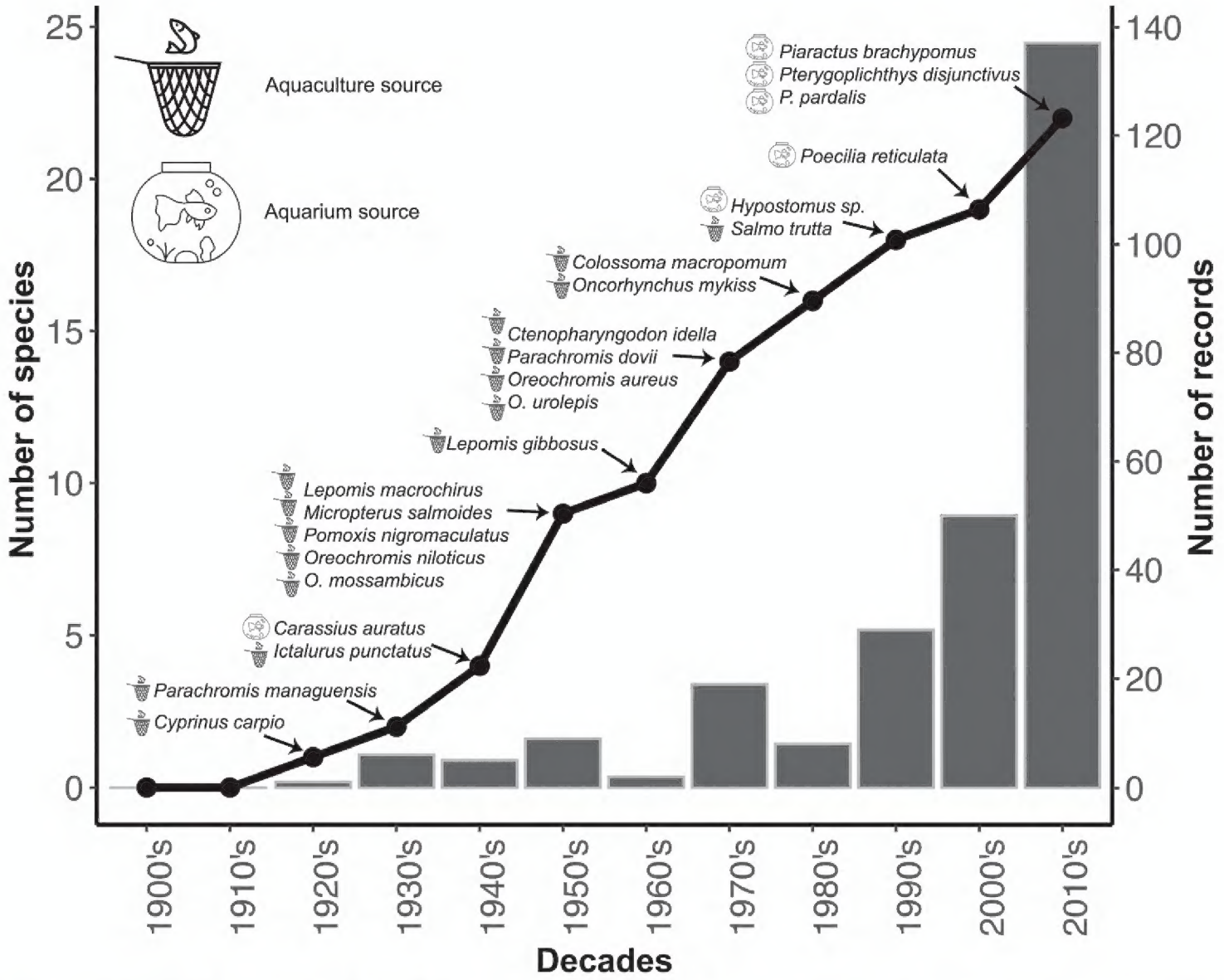

Figure 3. Cumulative number of non-native freshwater fishes (trend line) and the number of records (bars) in Guatemala through time since early 1900's. Number of species and records are grouped by decades.

sailfin catfish and Amazon sailfin catfish (*Pterygoplichthys disjunctivus* and *P. pardalis*, respectively), and Pacu (*Piaractus brachypomus*) (Fig. 3; Table 1). The number of records has increased with time, with a striking increase in the past 20 years (Figs 2, 3).

From the 22 species of NNFF introduced in Guatemala, we identified that 73% (16 species) were introduced from an aquaculture source and 27% (six species) of the introductions are from an aquarium source (Fig. 3; Table 1). A total of four (18% of total) species of NNFF were introduced in Guatemala during the Pre-1950 period (Fig. 3). Three of these introductions were of species from aquaculture source and only one is from aquarium source (Fig. 3; Table 1). During the 1950–1999 period, 14 NNFF (64% of total) were introduced in Guatemala (Fig. 3). Thirteen of these introductions were from aquaculture source and only one from aquarium source (Fig. 3; Table 1). Finally, during the contemporary period, four species (18% of total) have been recorded in Guatemala and all these species were identified as introductions from an aquarium source (Fig. 3; Table 1). Twelve NNFF were identified to have established populations (see methods) in various aquatic systems in Guatemala (Table 1). Four NNFF were assessed as not established, and the establishment status of the remaining six recorded NNFF in Guatemala is unknown (Table 1).

Table 2. Recorded non-native freshwater fishes and the cumulative number of species per river sub-basin in Guatemala. 1 = presence, 0 = no recorded. The number in parentheses correspond to the numbering of river -sub-basin in Fig. 1.

Drainage	Pacific coast								Atlantic coast							Gulf of Mexico						
sub-basin	Río Ocosito-Naranjo (3)	Río Samalá (4)	Río Nahualate (6)	Lago de Atitlán (7)	Río María Linda (11)	Río Los Esclavos (12)	Río Paz (13)	Río Lempa (14)	Río Motagua (15)	Río Cahabón (16)	Río Polochic (17)	Lago Izabal-Río Dulce (18)	Río Sarstún (19)	Río Mopán-Belice (22)	Río Hondo (23)	Río San Pedro-Candelaria (24)	Río Usumacinta-main channel (25)	Río La Pasión (26)	Río Ixcán (29)	Río Nentón (31)	Río Salinas – Chixoy (27)	No. River sub-basins present
Total no. of species per river sub-basin	2	1	1	9	8	3	2	3	5	5	3	6	1	1	1	8	2	5	1	1	6	
Cyprinidae																						
Carassius auratus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	2
Cyprinus carpio	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	4
Xenocyprididae																						
Ctenopharyngodon idella	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	4
Serrasalmidae																						
Piaractus brachypomus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Ictaluridae																						
Ictalurus punctatus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	2
Loricariidae																						
Pterygoplichthys disjunctivus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
Pterygoplichthys pardalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2
Pterygoplichthys sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	4
Hypostomus sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Salmonidae																						
Oncorhynchus mykiss	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Poeciliidae																						
Poecilia reticulata	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2
Centrarchidae																						
Lepomis gibbosus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Lepomis macrochirus	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Micropterus salmoides	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	4
Pomoxis nigromaculatus	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2
Cichlidae																						
Parachromis dovii	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Parachromis managuensis	1	1	0	1	1	1	1	1	1	1	1	1	0	0	0	1	0	1	0	0	1	14
Oreochromis aureus	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	1	1	1	0	0	0	7
Oreochromis mossambicus	0	0	0	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	1	7
Oreochromis niloticus	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	3
Oreochromis sp.	1	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0	1	1	0	7

Distribution of non-native freshwater fishes in Guatemala

Non-native freshwater fishes were recorded in 21 of the 33 (64%) river sub-basins in the country (Figs 2, 4, Table 2). The Lago de Atitlán sub-basin (Pacific coast drainage) possess the highest number of NNFF (nine species), followed by the Río María Linda (Pacific coast drainage) and Río San Pedro-Candelaria (Gulf of Mexico drainage) river sub-basins with eight species each (Fig. 2D). The Río Salinas-Chixoy (Gulf of Mexico drainage) and the Lago de Izabal-Río Dulce (Atlantic coast drainage) river sub-basins

have reported six species each (Figs 1, 2D; Table 2). In contrast, the river sub-basins in western Guatemala possess the lowest number or zero records of NNFF (Fig. 2D).

Three families (i.e., Cichlidae, Loricariidae, and Cyprinidae) are the most widespread groups of NNFF with records across the three major drainages in Guatemala (Fig. 4; Table 2,). Non-native cichlids possess records in 19 (58%) of the river sub-basins (Fig. 4A, B; Table 2). Overall, Tilapias are distributed in 18 (55%) of the river sub-basins (Fig. 4A; Table 2), followed by the Jaguar guapote (*P. managuensis*) which is present in 14 (42%) river sub-basins (Fig. 4B; Table 2). The armored catfishes (Loricariidae), despite being "recently" introduced (in the past 30 years; Fig. 3) are the second most widespread group. Armored catfishes have been recorded in eight (24%) river sub-basins (Fig. 4C; Table 2). Here we present the first vouchered record of *Pterygoplichthys* sp. (USAC 2422) in Río María Linda river sub-basin in the Pacific coast drainage in southern Guatemala (Fig. 4C; Table 2). Finally, Carps (Cyprinidae) are reported in six (18%, Fig. 4D; Table 2) river sub-basins across the country.

Four families (i.e., Centrarchidae, Poeciliidae, Ictaluridae, and Xenocyprididae) have been recorded in two major drainages in Guatemala (Fig. 4; Table 2). The Largemouth bass and Sunfishes (Centrarchidae) are recorded from six (18%, Fig. 4E; Table 2) river sub-basins. The Grass carp (Xenocyprididae) is reported from four (12%, Fig. 4D; Table 2) river sub-basins. In contrast, the Guppy (Poeciliidae) and the Channel catfish (Ictaluridae) are reported from only two river sub-basins each, while the Rainbow trout and Pacu are reported only from one river sub-basin each in the Gulf of Mexico drainage (Fig. 4F). The species Wami tilapia, Sea trout, and Tambaqui were excluded from the distribution analysis because they do not possess reliable geo-referenced data (see methods).

Discussion

Non-native freshwater fishes and their source of introduction

Our work identified the introduction of 22 NNFF in Guatemala, adding seven species (i.e., *Colossoma macropomum*, *Hypostomus* sp., *Lepomis gibbosus*, *Oreochromis niloticus*, *O. urolepis*, *Parachromis dovii*, and *Salmo trutta*) to previous reports for the country (see Kihn-Pineda and Cano 2012; Elías et al. 2018; Gaitán et al. 2020). We identified aquaculture as the main source of introduction of NNFF (73%, Fig. 3; Table 1) supporting our hypothesis. Introductions for aquaculture purposes are mainly driven by governmental goals to develop pisciculture and fisheries for food security in the country (Holloway 1950; Hughes 1974). This pattern is consistent with what is observed in several Latin American countries (e.g., Nicaragua, McCrary et al. 2007; Brazil, Ortega et al. 2015; Forneck et al. 2021), where pisciculture was implemented as a strategy for ensuring food security during the early 1950s (Miles 1967; Canonico et al. 2005). Although records of introductions of NNFF in Guatemala date back prior to the 1950s (Fig. 3) the purposes of some of these early introductions are not well documented (e.g., Common carp).

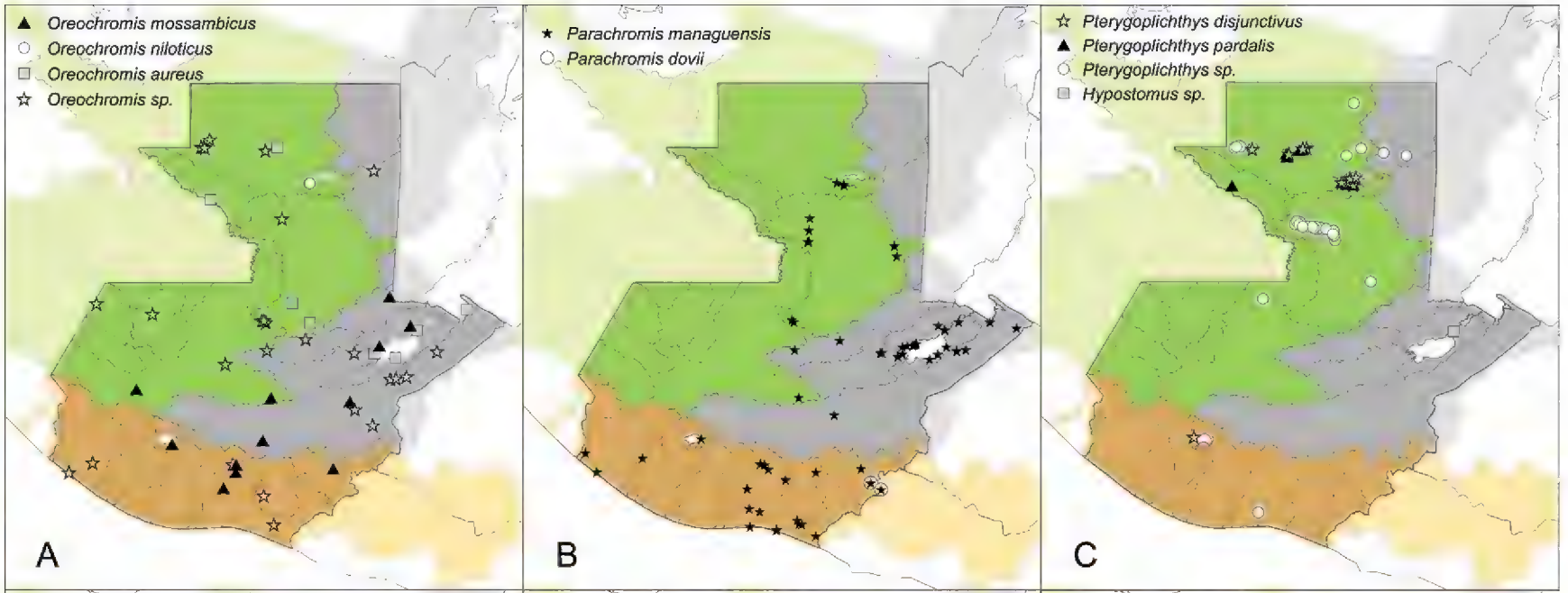

Figure 4. Distribution of non-native fishes in Guatemala, classified by Family. **A and B)** Cichlidae, **C)** Loricariidae, **D)** Cyprinidae and Xenocyprididae, **E)** Centrarchidae, **F)** Salmonidae, Ictaluridae, Serrasalmidae and Poeciliidae. Pacific coast drainage (light brown), Atlantic coast drainage (grey), and Gulf of Mexico drainage (green).

We identified that the majority of non-native species of cichlids (five species), centrarchids (three species), and cyprinoids (two species) that have been introduced for aquaculture purposes are now established (sensu Blackburn et al. 2011; Table 1) in several aquatic systems in Guatemala (e.g. juveniles and individuals in reproductive stages have been collected and observed; authors' field observations; Fig. 4A, B, and D). The species *L. gibbosus*, *S. trutta*, and *O. urolepis* were classified as not established since we did not find evidence of their presence in aquatic ecosystems in Guatemala after their record of introduction (Suppl. material 1: Table S1). In contrast, the status of *I. punctatus*, *O. mykiss*, and *C. macropomum* was assessed as unknown (Table 1). For example, the Rainbow trout (*O. mykiss*) is currently cultivated in aquaculture farms in the highlands of central and western Guatemala (López Paredes 2013; FAO 2018) and the potential for their escape (Crawford and Muir 2008; Arismendi et al. 2009) into the aquatic systems in this region remains.

Six species that are common in the aquarium trade have been collected in the aquatic ecosystem in Guatemala (Fig. 3; Table 1). Our temporal analysis identified aquarium release as the common source of introductions of NNFF in Guatemala during the past 20 years (Fig. 3). *Carassius auratus* and *Hypostomus* sp. are the only two species from the aquarium source that were introduced prior to the year 2000 (Fig. 3; Table 1). The remaining four introduced aquarium species were reported during the past 20 years (Kihn-Pineda et al. 2006; Kihn-Pineda and Cano 2012; Penados Saravia 2014; Elías et al. 2018; Gaitán et al. 2020), highlighting the aquarium trade as a potential source of new introductions due to bad practices (e.g., intentional release by aquarium hobbyists; Duggan et al. 2006) or the increase of aquarium trade in Guatemala. Although there is no evidence of established populations (sensu Blackburn et al. 2011) of *C. auratus*, *Hypostomus* sp., *Piaractus brachypomus*, or *Poecilia reticulata* in Guatemala, these species have successfully established populations in other parts of the world (e.g., Lindholm et al. 2005; Schofield et al. 2006; Pound et al. 2011; Correa et al. 2014; Oliveira et al. 2014), underscoring the need for active monitoring in the waterbodies where these species have been reported.

In contrast with the other species introduced by aquarium release, the Vermiculated sailfin and the Amazon sailfin catfish are a major concern in Guatemala and the region due to their rapid geographic expansion. The records of these species suggest that the sailfin catfishes (*Pterygoplichthys* spp.) first entered Guatemala via the lower reaches of the Usumacinta River in southern Mexico, where their establishment was previously reported (Wakida-Kusunoki et al. 2007). Subsequently, the sailfin catfishes have invaded the upper reaches of the Usumacinta River (i.e., La Pasión and Salinas-Chixoy river sub-basins in Guatemala; Fig. 4C). The sailfin catfishes have established populations (*sensu* Blackburn et al. 2011) in five river sub-basins in northern Guatemala (Fig. 4C) in the last ten years without human assistance (Barrientos and Quintana 2012; Ariano-Sánchez et al. 2017; Barrientos et al. 2018; Gaitán et al. 2020). Based on the evidence of established populations and active dispersal (see Schmitter-Soto et al. 2015; Gaitán et al. 2020), we considered the sailfin catfishes a regional invasive species (sensu Blackburn et al. 2011).

In addition, here we report the first record of one individual of *Pterygoplichthys* sp. (USAC 2422) in the María Linda river sub-basin in the Pacific coast drainage (Fig. 4C). We hypothesized that the latter introduction and the records of Armored catfishes in Lago de Atitlán (Villavicencio 2017) and Lago Izabal–Río Dulce sub-basins (Fig. 4C) are due to isolated local aquarium release and are not related to the established populations in northern Guatemala, but further research is needed. Moreover, some established populations of sailfin catfish in southern Guatemala are reported by fishermen, but future collecting efforts in river sub-basins in the Pacific slope are needed for corroboration.

Distribution of non-native fishes in Guatemala

Non-native fishes are currently recorded from 64% river sub-basins in Guatemala and our data shows the geographic expansion of NNFF through time (Fig. 2). The river sub-basins with the highest number of NNFF reported are the Lago de Atitlán (n = 9 species), María Linda (n = 8 species) in southern Guatemala, and Río San Pedro-Candelaria in the north (n = 8; Fig. 2, Table 2). We suggest that the 12 (36%) river sub-basins that do not possess records of NNFF (Fig. 2D) are under-sampled, hindering our understanding of how widely distributed NNFF are in the country. The paucity of collection records, particularly in western Guatemala, can be explained by a scarcity of ichthyological exploration since the 1960s. Thus, records of fishes in this region are underrepresented in scientific collections over the last 50 years (Quintana et al. 2016). The Hondo River basin is a trinational watershed that is shared with Mexico and Belize that occupies the most northeastern corner of Guatemala (i.e., Río Hondo river sub-basin; Fig. 1). Sailfin catfishes have been recently reported in this river sub-basin (see Gaitán et al. 2020), however, the Río Hondo sub-basin is likely under-sampled relatively to other northern Guatemalan river sub-basins (e.g., Río La Pasión and Río San Pedro-Candelaria). Tilapias (*Oreochromis* sp.) have been reported in the Hondo River in Belize and Mexico (Esselman et al. 2013; Schmitter-Soto et al. 2015) but we did not find records of Tilapias in the Hondo sub-river basin in Guatemala. We hypothesize that at least one species of the genus *Oreochromis* is present in the Río Hondo river sub-basin within the political boundaries of Guatemala due to the connectivity of the river networks. The absence of records of Tilapias (Fig. 4B) in this river sub-basin is due to the lack of sampling effort in aquatic systems in this region of Guatemala. Furthermore, Schmitter-Soto et al. (2015) hypothesized that the source of the Amazon sailfin catfish in the Hondo River in Mexico and Belize was the Lake Petén Itzá located in the neighboring river sub-basin (i.e., San Pedro-Candelaria; Fig. 1). This highlights the importance of implementing multinational collaborations to better understand the problematic nature of non-native species in northern Central America and southern Mexico.

The Jaguar guapote is the most widespread NNFF in the country (Fig. 4B; Table 2). Juvenile specimens of this species have been found in some localities, indicating established populations in large ecosystems (e.g., Barrientos and Allen 2008).

Tilapias are the most widespread non-native group of fishes in the country (18 sub-basins; Fig. 4A). Despite their introduction having started at least two decades after the introduction of the Jaguar guapote (Fig. 3), Tilapias have been farmed for over 60 years and had become one of the most important and extensively used species in aquaculture across the country (López Paredes 2013; Palomo Cortez et al. 2016; FAO 2018; García-Pérez et al. 2021). The extensive use of Tilapias has led to the spread of established populations in several river sub-basins across the country (authors' field observations). Similarly, the Common carp and the Grass carp are the most widespread cyprinoids in Guatemala, with established populations across the country. Juveniles and females in the reproductive stage of these two species have been observed in at least three sub-basins (i.e., Cahabón, Salinas-Chixoy, and San Pedro-Candelaria river sub-basins; authors' field observations). Furthermore, The Common carp is considered of economic importance in artisanal fisheries (Muñoz 2018). Conversely, the Goldfish was reported only in two river sub-basins and has not been collected since 1971.

Centrarchids are mainly distributed in river sub-basins of the Pacific coast drainage (Fig. 4E). Most of the records correspond to the Lago de Atitlán sub-basin, particularly in Lake Atitlán, where the first ones were introduced (Holloway 1950). Populations of centrarchid species have now been established and support the local fisheries in Lake Atitlán (Barrientos and Quintana 2012). Outside Lake Atitlán, the distribution of centrarchids in Guatemala is narrow, with Sunfishes (*L. macrochirus* and *P. nigromaculatus*) known from only two river sub-basins and Largemouth bass distributed in three river sub-basins in Guatemala (Fig. 4E).

The sailfin catfishes, Vermiculated sailfin and Amazon sailfin, are widely distributed in several river sub-basins (Fig. 4C) of the Usumacinta River in northern Guatemala. The first report of a sailfin catfish in Guatemala was in the San Pedro-Candelaria river sub-basin in 2009 (see UNIPESCA 2010), erroneously identified as *Hypostomus plecostomus*, subsequently sailfin catfishes were reported from La Pasión river sub-basin in 2011 and more recently from Lake Lachuá (Ariano-Sánchez et al. 2017) in the Salinas-Chixoy river sub-basin, Lake Atitlán (Villavicencio 2017) located in the Lago de Atitlán river sub-basin, and in northeastern Guatemala (Gaitán et al. 2020). However, anecdotal reports of sailfin catfishes continue to appear in other river sub-basins across the country. One species of armored catfishes, *Hypostomus* sp. is only known from a single record in Lake Izabal located in the Lago de Izabal-Río Dulce sub-basin from 1996. Despite recent ichthyological fieldwork in this river sub-basin (e.g., Barrientos and Allen 2008; Quintana and Barrientos 2011) this species has not been subsequently reported. Also, the new report of *Pterygoplichthys* sp. (USAC 2422) in the María Linda river sub-basin highlights the potential threat of expansion of this invasive species across the Pacific coast drainage, similar to the invasion observed in northern Guatemala (see discussion above). It is important to highlight that approximately 69% of sailfin catfishes' records are only identified to the genus level (*Pterygoplichthys* sp.) due to the difficulty in correctly identifying this taxonomic group to species level (J. Armbruster pers. comm.).

Management

The lack of previous research and systematic control of activities such as stocking, establishment of new fish farms, and farms monitoring, etc., has hampered our understanding of the spread of NNFF and their potential threat to native fish fauna and aquatic ecosystems. The composition and distributional patterns of NNFF in Guatemala primarily stem from four main factors. First, governmental strategies for aquaculture and restocking, supported in many cases by international cooperation (UNIPESCA 2008, 2010; CONAP 2011; López Paredes 2013; FAO 2018). Second, there is a lack of management and control of unintentional releases from aquaculture farms. Third, riverscape connectivity across political boundaries allows the dispersal of non-native species (Schmitter-Soto et al. 2015; Esselman et al. 2013); and fourth, intentional releases of ornamental fishes by aquarium hobbyists (Elías et al. 2018).

At least two government agencies oversee the supervision of activities related to NNFF, and although there are recommendations and regulations for the management of non-native species in place (CONAP 2011), there is a notorious lack of enforcement (Soto Coronado 2017). Moreover, there are international agreements to control potential invasive species that are not being implemented (e. g. the Convention on Biological Diversity, Ramsar Convention on Wetlands of International Importance; Ciruna et al. 2004; Burgiel et al. 2006).

Non-native freshwater fishes in northern Central America are of multi-national political concern because several river basins in the region are shared among neighboring countries (e.g., the Usumacinta and Motagua Rivers; Fig. 1) and non-native species continue to be reported in the region (e.g., Elías et al. 2018; Lardizabal et al. 2020; Álvarez-Pliego et al. 2021). The tilapia and carp stocking and aquaculture have been promoted by the Mexican government in the southern region, particularly within Usumacinta river basin, which is shared among Mexico, Guatemala and Belize (Suarez 2011; Amador-del-Ángel and Wakida-Kusunoki 2014). Since political boundaries do not act as dispersal barriers, NNFF can freely move across aquatic systems within the Usumacinta riverscape. For example, the spread of Tilapias has been documented in the Río Azul basin shared between Mexico and Belize (Esselman et al. 2013). However, the connectivity among established populations of Tilapia has not been evaluated from a regional perspective. We suggest that a regional scale approach to this problem would be beneficial to reduce the introduction of NNFF, rather than a country-by-country one. A regional approach can provide a better understanding of the status of NNFF and would lead to a more integrated and effective management of the shared aquatic systems and resources in the region. Regional management strategies should include the regulation of aquarium trade and promote the education of aquarium hobbyist to prevent further introductions of NNFF in the wild. Moreover, policies regarding the use and stocking of NNFF in river sub-basins that are shared with neighboring countries should be considered in international agreements, because it creates a regional concern (e. g. Mexico, Belize, Honduras and El Salvador, Fig. 1; Granados et al. 2000).

Effects of non-natives fishes in aquatic ecosystems in Guatemala

The negative impacts of NNFF introductions have been documented in a few cases. Ichthyologists have hypothesized that the fish assemblage of the closed basin of the crater Lake Atitlán was composed of "small" native fishes that were translocated from nearby rivers (Meek 1908; Miller 1955). Thus, the Guatemalan government, advised by US Fish and Wildlife Service, proposed the introduction of "large" fish, such as Largemouth bass, Crappy, and Bluegill, to supplement sources of protein for the nearby communities (Holloway 1950). Zaret and Paine (1973) pointed out that these introductions had several unforeseen ecological costs, such as the extinction of the small native fish and crabs, and produced minimal benefits for the locals, who were not familiar with how to "catch" centrarchids fishes. Moreover, the introduction of Largemouth bass was hypothesized to be a co-factor in the extinction of the Atitlán grebe (*Podilymbus gigas*), through overlapping on their food resources and direct predation according to LaBastille (1974) and Hunter (1988). Nowadays, the artisanal fishery in Lake Atitlán depends exclusively on centrarchids and local crabs (*Potamocarcinus magnus* and *Raddaus bocourti*; Barrientos and Quintana 2012; Wehrtmann et al. 2016).

The negative effects of other NNFF in the country have not been assessed; however, several species are known to be detrimental to ecosystem functioning and native fauna. For example, sailfin catfishes can cause river bank erosion, reduction of primary productivity, and changes in nutrient cycling dynamics (Capps and Flecker 2013a, 2013b, 2015; Capps et al. 2015) as well reducing the diversity of the assemblages of native fishes (Escalera-Vázquez et al. 2019). The sailfin catfishes which are abundant in large tributaries of the Usumacinta basin (e.g., La Pasión and San Pedro-Candelaria river sub-basins) have become a common prey for river otters (*Lontra longicaudis*; Juárez-Sánchez et al. 2019). This new predator-prey interaction has reduced the trophic level and niche breath of river otters (Juárez-Sánchez et al. 2019). Other examples are the carps which can dramatically modify the ecosystem by reducing the availability of macrophytes, reducing water quality, and affecting the plankton community (Matsuzaki et al. 2009). These changes in habitat structure and ecosystem interactions will likely affect the recruitment for fish in different systems (Barrientos and Allen 2008).

Historically, introductions have been practiced for almost 100 years, and most of these fishes have likely become part of the fish assemblages in the regions where they have been introduced. Several introduced species in Guatemala, such as Jaguar guapote, Tilapias, and Grass carp, are currently important if not pivotal to artisanal fisheries (Quintana and Barrientos 2011; Barrientos et al. 2018) and can be found in artisanal fish markets throughout the country.

Conclusions

Our contribution to the analysis of NNFF introductions and patterns of distribution provides a first step towards better understanding the composition and persistence of non-native fishes across the country. The spread of NNFF found in our analysis

underscores the need to increase a systematic control of introductions, particularly those resulting from aquarium release that are becoming more frequent. Even though NNFF are commonly used for enhancing artisanal fisheries and aquaculture projects, some of these species can be harmful to freshwater ecosystems (Vitule et al. 2009), therefore, the increase of sustainable management of fisheries based on native species is critical. The gaps found in this analysis and the potential negative effects of non-native fishes indicate that there is a need for systematic fish fauna monitoring, as well as ecological research of aquatic ecosystems and their biota, to detect conservation threats, including the impacts of non-native fishes. These efforts are especially needed in river sub-basins where more NNFF are reported, where non-native species that are capable of modifying ecosystems (e.g., Sailfin catfishes) are present, and in those river sub-basins with a high proportion of endemisms (see Elías et al. 2020).

The lack of applied integrative management in environmental policies and the objectives of the Guatemalan Fishing Agency in Guatemala, creates a conflict of interest that needs to be resolved to fulfill national conservation goals and comply with international treaties (i.e., Convention on Biological Diversity). A comprehensive plan involving interested parties in this matter is key to ensuring the control and management of non-native fishes. This plan could help to prevent and mitigate the impact of potentially invasive fishes and their negative effects on native biota, and to distribute the resources needed to make this task more efficient. As recent dispersals and new records continue to occur, it is urgent to look ahead to new and more adequate decision-making tools, and to develop public awareness measurements that address both the socio-economic and conservation needs of developing countries.

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Supplementary material 1

Table S1

Authors: César E. Fuentes-Montejo, Diego J. Elías

Data type: Occurrences

Explanation note: Supplementary material contains the curated dataset of non-native freshwater fishes in Guatemala analyzed.

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